

THE POTENTIALITIES AND LIMITATIONS OF WOOD
ANATOMY IN THE STUDY OF THE PHYLOGENY
AND CLASSIFICATION OF ANGIOSPERMS

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VESSELS

IN OUR RECONNAISSANCE of the tracheary cells of the vascular land plants (Bailey and Tupper, 1918), which led to so many subsequent investigations of evolutionary trends in the xylem of angiosperms, we presented two types of evidence. (1) *Intensive* investigations were made of variations in the size, form and pitting of tracheary cells in different parts of the same plant and in different plants of the same species grown under varying environmental influences. (2) *Extensive* comparative data, obtained from a wide range of randomly selected representatives of the gymnosperms and dicotyledons, were statistically analyzed and tabulated. The latter data, in spite of demonstrated variations within single plants and single species, revealed surprisingly consistent changes in the size, form and pitting of tracheary cells at successive levels in the evolution and specialization of vessels in the dicotyledons as-a-whole.

Similar evolutionary trends in the development and specialization of vessels in the primary xylem of monocotyledons have been demonstrated by Cheadle (1942, 1943a, 1943b, 1944).

At present, the development and specialization of vessels in dicotyledons and monocotyledons provide two of the most, if not the most, comprehensive and reliable evolutionary trends that are preserved in surviving representatives of the angiosperms. It should be recognized in this connection that no longer are there uncertainties regarding the directions in which the evolutionary trends are progressing. This is due to the obvious fact that the structure of geologically ancient land plants negates any possibility of deriving tracheids from vessels. As re-emphasized by Frost (1930a, 1930b, 1931), since vessels clearly evolve by modification of tracheids, the most primitive vessels are composed of members which closely resemble tracheids in size, form and pitting. The most highly specialized vessels are those whose constituent tracheary cells least resemble tracheids.

The most primitive vessels in the metaxylem and secondary xylem of dicotyledons and in the metaxylem of monocotyledons are composed of members which closely resemble thin-walled, scalariformly pitted tracheids. Thus, the vessel-members are long, comparatively slender in relation to their length, and (as viewed in tangential longitudinal sections of the xylem) have gradually tapered, extensively overlapping ends. They are thin-walled and angular in cross-sectional view. They differ from tracheids

at functional maturity solely in the dissolution of pit membranes in a number of the bordered pit pairs in their overlapping ends. In the secondary xylem of dicotyledons, such vessels are more or less uniformly distributed and are infrequently in contact laterally with one another. However, where lateral contacts do occur the intervascular imperforate pitting is scalariform.

The members of the most highly specialized vessels — in contrast to those of the most primitive ones — are short, comparatively broad for their length and tend to be oval or circular in cross-sectional view. They have truncated ends regardless of variations in their diameter. There is a single perforation at each end of the cell. The vessels commonly tend to be more or less extensively aggregated in the secondary xylem, and the intervascular pitting is alternating-multiseriate.

In view of such structural differences as these, it is possible to arrange the vessels of both the dicotyledons and monocotyledons in evolutionary trends of increasing specialization. It is important to bear in mind that this can be accomplished *entirely independently* of the various systems of classifying the taxa of angiosperms, thus avoiding circular arguments based upon assumptions regarding the primitive or specialized character of various representatives of the angiosperms. In other words, primitive vessels are distinguished from specialized ones *solely* upon their own structural differences, and *entirely* without reference to the putative primitiveness of the plants in which they occur.

PARALLEL AND CONVERGENT EVOLUTION IN VESSELS

Comprehensive summations of evidence now indicate that there has been an independent, but parallel, evolution of vessels in dicotyledons and monocotyledons, Bailey (1944), Cheadle (1953). Therefore, if the angiosperms are monophyletic, the monocotyledons must have been derived either from vesselless dicotyledons or from common vesselless ancestors. Furthermore, in both of the principal divisions of the flowering plants, as in *Selaginella* and *Pteridium*, vessels evolved by modification of scalariformly pitted tracheids, in striking contrast to the Gnetales where vessels evolved from tracheids having circular bordered pits with conspicuous tori. Thus, available evidence negates any possibility of deriving the angiosperms from the Gnetales, Coniferales, Taxales or Ginkgoales. The similarity between the highly specialized vessels of *Gnetum* and of certain dicotyledons is owing to convergent, rather than parallel, evolution.

The wide range of variability in the reproductive organs of vesselless dicotyledons suggests that vessels may have originated more than once in primitive representatives of the dicotyledons. In addition, much evidence is now available which demonstrates that similar trends of specialization of vessels have occurred independently in many families of the dicotyledons. In other words, similarities due to parallel evolution are surprisingly common in the xylem of dicotyledons.

CORRELATIONS BETWEEN VESSELS, CAMBIAL INITIALS
IMPERFORATE TRACHEARY CELLS, WOOD PARENCHYMA
AND RAYS

In the case of the secondary xylem of dicotyledons, it is possible by statistical correlations to show that during the evolution and specialization of vessels there are concomitant changes in the fusiform initials of the cambium, Bailey (1920a, 1923), and also in the ground mass of imperforate tracheids which tend to assume an increasingly fiber-like form, Bailey and Tupper (1918), Bailey (1936). In addition, it is possible by statistical correlations to obtain significant clues regarding primitive forms of wood parenchyma (Kribs 1937) and wood rays (Kribs 1935, Barghoorn 1940, 1941a, 1941b), and to study a number of their salient trends of specialization.

CAMBIAL INITIALS

As in the case of vesselless dicotyledons and gymnosperms, the most primitive kinds of vessel-bearing secondary xylem are formed by a cambium having long fusiform initials with gradually tapered, extensively overlapping ends as seen in tangential sections. The anticlinal divisions of these initials are pseudo-transverse, and the resulting cells elongate extensively before they in turn divide anticlinally. Thus, there is a wide range of variability in the length of neighboring initials. Since the frequency of anticlinal divisions and the amount of apical elongation are not constant, the average or mean length of the fusiform initials varies markedly in different parts of a fully matured plant. The most significant of these variations is the increase in mean size during the lateral enlargement of stems, due largely to an increase in mean length of the fusiform initials, but also to a less conspicuous increase in their tangential diameter. Important also are reductions in length of initials at nodes as contrasted with internodes of young stems, at the junctions of large stems with branches or roots, and in burly tissues due to injuries or other abnormalities. Furthermore, dwarfing due to extremely retarded growth in unfavorable habitats reduces the mean size more or less markedly. One should bear in mind in this connection that the fusiform initials continue to divide periclinally, thus forming tracheary derivatives, during their intervals of elongation between successive anticlinal divisions. Therefore, since vessel members elongate slightly, if at all, during tissue differentiation, their variations in length closely parallel the variations in length of the cambial initials.

Secondary xylem containing the most highly specialized vessels is formed by a cambium having short initials with abruptly tapered ends and slight overlap. The anticlinal divisions are radial longitudinal and, owing to the elimination of apical elongation between such divisions, the neighboring initials are of relatively uniform length and exhibit a stratified or storied arrangement in surface view of the cambium. The mean length of the

initials varies somewhat in different parts of a fully matured plant and in plants grown under different environmental influences, but the variations are slight in comparison with those that occur in primitive cambia of dicotyledons and gymnosperms. For example, in different parts of a vesselless tree (*Pseudotsuga menziesii*) selected for comparison, the mean lengths of the fusiform initials varied between 900 μ and 6000 μ , the shortest initial being 280 μ and the longest 8600 μ . In contrast to this, the mean lengths of the initials in different parts of a tree having a storied cambium (*Robinia pseudoacacia*) varied between 150 μ and 190 μ , the shortest initial having a length of 70 μ and the longest one a length of 320 μ .

As in the case of primitive vessels, the mean length of the members of highly specialized vessels closely approximates the mean length of the cambial initials. However, the girth of the vessel members presents an entirely different problem. In primitively vesselless forms of secondary xylem, the tangential diameter of the tracheids is determined by the tangential diameter of the fusiform initials, whereas the radial dimension is due largely to radial expansion during tissue differentiation. It is for this reason that the tracheids exhibit radial seriations in cross sections of the secondary xylem, except in certain cases where the seriations are disturbed by excessive intrusive elongation of the tracheids during tissue differentiation. Furthermore, as the tangential diameter of the fusiform initials tends to increase as a stem enlarges in circumference (Bailey, 1920b), the tracheids of the later-formed xylem tend to be correspondingly broader, as well as much longer, than they are in the first-formed secondary xylem. On the contrary, the girth of vessels is determined by both tangential and radial expansion during tissue differentiation. Where the vessel members are much broader than tracheids, as they so commonly are in highly specialized vessels, they afford no reliable clue regarding the tangential diameter of the cambial initials. It should be noted in passing that the girth of highly specialized vessels varies widely, not only in different taxa and in plants grown under different environmental conditions, but also in different parts of the same plant. The vessels of the later-formed secondary xylem commonly tend to be conspicuously broader than those of the first-formed secondary xylem (Bailey and Howard, 1941). However, such variations in girth are due largely to variations in the amount of lateral expansion during tissue differentiation rather than to differences in the diameters of cambial initials.

IMPERFORATE TRACHEARY CELLS

During the evolution of the taller vascular land plants, there has been a constant necessity of maintaining an equilibrium between rates of conduction and strength in stems (Bailey, 1953). Among vesselless gymnosperms, there is at times a more or less obvious tendency to form tracheids which vary in strength and in their permeability to ascending sap, certain of the

vertically contiguous tracheids being broader, thinner-walled and more profusely pitted, whereas others are more slender, thicker-walled and have a reduced number of relatively small, circular bordered pits. This tendency toward "division of labor" in conduction and strength is most obvious and sharply defined in gymnosperms having pronounced growth rings in their secondary xylem, viz. layers of relatively weak, highly permeable tracheary tissue alternating with dense much stronger ones.

In certain of the vesselless dicotyledons, as in certain of the Bennettiales (*sensu lato*), which do not have a conspicuously zonate secondary xylem, the broader, thinner-walled tracheids tend to have abundant scalariform pitting and to be more or less randomly or irregularly distributed throughout the groundmass of secondary xylem. On the contrary, in the vesselless dicotyledons, *Tetracentron* and *Trochodendron*, as in certain remarkable representatives of the Bennettiales (*sensu lato*) recently described by Hsui and Bose (1952) and Bose (1953), which have conspicuous growth layers, the broad, thin-walled tracheids of the early-wood have profuse scalariform pitting, whereas the slender, thick-walled tracheids of the late-wood are provided with a few, small, circular, bordered pits only.

If the vessels of dicotyledons were derived from scalariformly pitted tracheids in zonal arrangement, it might be anticipated that the most primitive vessels in the secondary xylem would be aggregated in concentric zones. This obviously is not the case, and indicates that they developed by modification of scalariformly pitted tracheids that were loosely diffused throughout the groundmass of thick-walled, mechanically stronger tracheids.

The division of labor between strength and conduction in tracheary cells becomes increasingly intensified during the evolution and specialization of vessels in the secondary xylem of the dicotyledons. As revealed by significant statistical correlations in the dicotyledons as-a-whole, the imperforate tracheids become increasingly fiber-like at successive levels in the evolutionary specialization of vessels and cambial initials, due to proportionally greater elongation during tissue differentiation and to reduction and elimination of borders about the pits.

Even during the earlier stages of the evolution of vessels, there is a tendency for enhanced elongation of the thick-walled tracheids during tissue differentiation, but it is not sufficient to compensate for the marked reduction in length of the cambial initials, i.e. when comparisons are made with vesselless dicotyledons and gymnosperms. As the specialization of vessels progresses, the elongation of the imperforate tracheary cells tends to become proportionally greater until elongations of several hundred percent are not infrequently attained. However, the enhanced elongation does not neutralize the shortening effect of excessive reduction in length of the cambial initials. Thus, the imperforate tracheary cells tend, in general, to become shorter as vessels attain successive levels of increasing evolutionary specialization.

WOOD PARENCHYMA

Wood parenchyma strands ordinarily do not elongate or enlarge their tangential diameter appreciably during tissue differentiation. Since their length and tangential diameter is determined largely by the cambial initials, their size and the size and number of their constituent cells decreases concomitantly with the reduction in size of cambial initials. It should be noted in this connection that, particularly in the case of highly specialized tracheary tissue, the wood parenchyma strands provide reliable clues regarding the dimensions of cambial initials. Furthermore, when they occur in extensive aggregations, they provide a means of determining whether the cambium is of a storied or non-storied type.

The distribution of wood parenchyma in vesselless dicotyledons varies between absent, scanty diffuse, diffuse-in-aggregates and narrow tangentially banded. It is not possible at present to determine with certainty whether absence of wood parenchyma in vesselless dicotyledons is a primitive or a derived condition. However, collateral evidence indicates that the tangentially banded parenchyma of *Pseudowintera* is derived by a modification of the diffuse pattern.

Among woods having primitive vessels, nearly 90 percent have diffuse parenchyma, commonly of the diffuse-in-aggregates type. Absence of wood parenchyma may approximate 10 percent, whereas narrow, tangentially banded apotracheal and scanty paratracheal types are of rare occurrence. Broad-banded apotracheal and abundant paratracheal forms of distribution occur in woods whose vessels have attained relatively high levels of evolutionary specialization. Various mixtures of apotracheal and paratracheal patterns are produced in association with transitional and highly specialized forms of vessels.

Although available statistical data (Kribs, 1937), demonstrate that the various forms of aggregated, apotracheal and paratracheal parenchyma are derived from a primitive, diffuse, apotracheal distribution, they do not provide a thoroughly reliable basis for arranging the diversified patterns in a single linear series of increasing structural specialization. Summations of morphological evidence from various taxa of the dicotyledons now indicate that reductions in the amount of wood parenchyma to terminal, scanty paratracheal, or absent occur independently at various levels of the evolutionary specialization of vessels. Uncertainties exist, however, in dealing with various mixtures of apotracheal and paratracheal parenchyma which may have developed in more than one way. For example, broad-banded apotracheal may have given rise to banded with included vessels, to aliform paratracheal to abundant vasicentric, or vasicentric paratracheal may have led to aliform to tangentially confluent, or both kinds of specialization may have occurred independently in different taxa. Such uncertainties cannot be clarified until more detailed and comprehensive studies have been made of a number of the larger families of the dicotyledons.

WOOD RAYS

Since the rays in secondary xylem are formed by ray initials of the cambium, their dimensions ordinarily are not directly influenced by those of the fusiform initials which form tracheary cells and wood parenchyma strands. However, owing to the fact that new ray initials are periodically formed by division of fusiform initials, there are at times indirect effects that should not be overlooked, particularly in the case of storied cambia.

The ray initials of vesselless dicotyledons and of dicotyledons having primitive forms of vessels are of two distinctly different shapes and aggregations. As viewed in tangential longitudinal sections, there are (1) erect ray initials in vertically uniseriate arrangement and (2) more nearly isodiametric ones in multiseriate aggregation. The multiseriate aggregations terminate both upward and downward in uniseriate extensions of erect initials. Two types of wood rays are formed by these initials, (1) high-celled uniseriate rays, and (2) multiseriate rays whose constituent cells are vertically short in comparison with those of the uniseriate rays except in their high-celled uniseriate extensions. These extensions appear to be uniseriate rays that are attached to the upper and lower margins of the multiseriate rays.

During the evolutionary specialization of vessels, divergent modifications of this primitive form of ray structure occur. Some of the more significant changes involve (a) reduction and elimination of multiseriate rays, (b) reduction and elimination of uniseriate rays, (c) reduction and elimination of all rays, (d) reduction in the height of ray cells with concomitant increase in their radial expansion during tissue differentiation, leading to the formation of so-called homogeneous rays, viz. composed throughout of more or less conspicuously "procumbent" cells, (e) excessive reductions or amplifications in the width of multiseriate rays, and (f) arrangement of low rays in transverse stratification where the secondary xylem is formed by a storied cambium.

Although transitional stages in the attainment of the end-products of each of these trends of specialization can be arranged in evolutionary series, the different trends of specialization cannot be combined in a single linear series which closely parallels that of the evolutionary specialization of vessels. Each trend of specialization, with the exception of storied rays, may occur at different levels of the increasing specialization of vessels.

THE ROLE OF WOOD ANATOMY IN TAXONOMY

Recognizing that the salient trends of evolutionary specialization in the xylem have been revealed by statistical analyses of the dicotyledons *as-a-whole*, the question arises, how and to what extent may they be utilized in studying relationships within orders, families, genera and species.

It is no longer justifiable to assume, as has so frequently been done in the past, that one organ or part of a plant is inherently more conservative and

reliable than are all others. From the point of view of the dicotyledons *as-a-whole*, it is evident that each organ or part may be relatively uniform morphologically in certain taxa whereas it is highly variable in others. Furthermore, the rates of evolutionary modification in different parts frequently are not closely synchronized. Thus, any particular evolutionary trend, however reliably established, applies to a single part of the plant *only* and does not *by itself*, provide a reliable basis for classifying the plants from which the evidence was obtained in a similar phylogenetic sequence, since evidence from other parts of the plant may negate such an arrangement. If a truly natural classification of dicotyledons is to be attained, it must be based upon harmonizing evidence from all organs and parts of the plants. It is in this synthesizing task that wood anatomy has a significant role in taxonomy.

There has been, and still exists, a tendency among those who concentrate their attention largely upon the study of wood anatomy to base conclusions regarding relationships and classification solely upon similarities and differences in the structure of the xylem. Such conclusions are unreliable unless supported by the totality of evidence from other parts of the plants. This is owing to the fact that similarities in the xylem, which may be due to parallel evolution, are not necessarily indicative of close genetic relationship of plants unless supported by strong corroborative evidence. Nor are conspicuous differences in the xylem necessarily indicative in all cases of remote relationship, since the evolutionary modification of the xylem may be accelerated in plants where a totality of evidence from all organs and parts is indicative of relatively close relationship.

Thus far, the evolutionary trends in the cambium and xylem of dicotyledons, when considered by themselves, have been most reliable and significant in *negations*. This is owing to the fact that plants which have retained primitive cambia and xylem cannot be derived from plants which have attained uniformly high levels of structural specialization. For example, the monocotyledons cannot be derived from the Ranunculaceae or Piperaceae. Within the dicotyledons, herbs, vines, lianas, succulents and many extreme xerophytes have attained high levels of tracheary specializations and cannot have given rise to trees and shrubs which retain relatively primitive forms of xylem. The relatively highly specialized xylem of the Amentiferae negates any possibility of considering them the primitive stock from which other dicotyledons have been derived.

There are certain details of the trends of specialization in the xylem which need to be more clearly and generally understood in shifting from a consideration of the dicotyledons *as-a-whole* to investigations of the taxonomy of individual taxa of restricted size. In revealing salient trends of evolutionary specialization by analyses of data obtained from the dicotyledons *as-a-whole*, variations due to obtaining specimens from different parts of the plant, from plants of different growth rates, from genetically differ-

ent taxa, etc., tend to neutralize one another. In addition, various localized, divergent trends of specialization do not obscure or confuse the major trends of evolution in the dicotyledons *as-a-whole*. However, when one becomes concerned with taxa of decreasing size, viz. families, subfamilies, tribes, genera and species, such variations and deviations become increasingly significant.

DEVIATIONS IN THE SYNCHRONIZATION OF STRUCTURAL CHANGES IN TRACHEARY CELLS

When *averaged* data are obtained from the dicotyledons *as-a-whole*, the successive evolutionary modifications of the cambium and of the length, form and pitting of its tracheary derivatives tend *in general* to be relatively closely synchronized in passing from the most primitive to the most specialized conditions. It should be kept in mind in this connection, however, that changes in the form, perforations and imperforate intervascular pitting of vessel members tend to be retarded in the metaxylem and first-formed secondary xylem (Bailey, 1944), as also not infrequently in the vessels of smaller diameter in the later-formed secondary xylem. Furthermore, there are families and genera in which one or another of the generally coordinated changes is accelerated or retarded in relation to the others. For example, accelerations in the transformation of scalariform to simple perforations, coupled with retardation in the lateral enlargement of vessels, may at times lead to the formation of relatively long vessel members with steeply inclined, rather than transversely oriented, simple perforation plates. Conversely, excessive enlargement of vessels, coupled with retarded changes in the perforations, may result in broad vessel members with nearly transversely oriented scalariform perforation plates. Precocious enlargement of vessels in vines and lianas, with concomitant changes in perforations and intervascular pitting, results at times in vessel members that are excessively long for their general level of morphological specialization. Conversely, extreme dwarfing, coupled with retardation of changes in perforations and intervascular pitting, frequently leads to the formation of vessel members that are short for their general level of primitive morphological structures. The changes in perforations and in intervascular pitting may be retarded or accelerated in relation to one another, as may those that occur in vessels as contrasted with imperforate tracheary cells.

In view of the occurrence of such localized variations as these, it is evident that considerable caution must be exercised in attempting to arrange the tracheary tissues of the species of a given genus or the genera of a particular family in linear evolutionary series which provide reliable evidence in discussions of relationships, particularly in taxa whose representatives fall within a relatively narrow range of the evolutionary specialization of vessels, e.g. Compositae, Leguminosae, etc. In the case of such taxa, undue emphasis should not be placed upon differences in the dimensions of tracheary cells, in the inclination of perforations, or in the character of inter-

vascular pitting in *randomly collected samples* of various species and genera. Detailed and laborious consideration must be given to the ranges of variability within each plant and within each species if comparable statistical averages are to be obtained.

LOCALIZED DIVERGENT TRENDS OF SPECIALIZATION

It is evident that in dealing with wood rays and with patterns of wood parenchyma distribution one is concerned with a number of divergent trends of specialization rather than with single unidirectional series of increasing evolutionary modification. Each of these trends of modification may occur independently at different levels of the structural specialization of vessels. In other words, parallel evolutionary changes in wood rays and wood parenchyma occur independently in many taxa of the dicotyledons.

Although the major trend of specialization in fusiform initials and in their tracheary derivatives is unidirectional, there are various localized divergent specializations which merit careful consideration in the discussion of taxonomic problems. For example, the tendency to form "tertiary" helical thickenings in tracheary cells is a divergent trend of specialization that has occurred independently in gymnosperms as well as in many taxa of the dicotyledons. Their presence in vessels is not indicative necessarily of close genetic relationship. Nor can it be assumed that such vessels are derived from tracheids with helical thickenings. Another common divergent trend of specialization is the tendency of imperforate tracheary cells to retain their living contents which divide forming septa internal to the lignified secondary wall. Such septate fiber-tracheids and libriform fibers, which function in storage of starch, crystals, etc. as well as mechanically, develop independently at various levels of the evolutionary specialization of vessels. Their occurrence in different taxa is not indicative necessarily of close taxonomic affinities.

Excessive thickening or attenuation of the walls of tracheary cells, unusual enlargement or reduction in the diameter of vessels, and unusually extensive aggregations of vessels in diversified patterns are of not infrequent occurrence in various taxa of the dicotyledons. It is advisable to deal with such structural modifications in terms of localized divergent specializations rather than to endeavor to incorporate them as parts of a single major unidirectional trend of evolutionary specialization. For example, there are taxa whose vessel members have attained relatively high levels of structural specialization as regards their length, form, perforations and pitting, but the vessels are thin-walled and angular in cross-sectional view. *A priori* the latter diagnostic feature might be interpreted as a retention of a primitive structural character. However, summations of evidence in various taxa indicate that there has been a reversionary trend of specialization to a thin-walled angular condition.

The formation of so-called vascular tracheids and vasicentric tracheids similarly represents divergent trends of specialization that occur independently in various taxa. By classical definition, these cells are included

in a broad general category of tracheary elements. However, they do not provide a sound basis for concluding that the evolution of vessels from tracheids is a truly reversible process. This is due to the fact that the end products of these trends of specialization differ markedly from the typical tracheids of vascular land plants in form and in their behavior during tissue differentiation.

CONCLUSIONS

The chief trends of evolutionary specialization in the cambium and xylem of dicotyledons are now so reliably established (except in the case of certain patterns of wood parenchyma distribution) that they can be utilized to advantage in studying salient problems of phylogeny and classification. When considered by themselves, they are most significant in *negations*, since a taxon which retains primitive forms of cambium and xylem cannot be derived directly from a taxon which has attained a uniformly high level of structural specialization. Unfortunately, owing to the frequent occurrence of parallel evolutionary changes, they cannot be utilized in *positive* assertions of relationship or phylogenetic derivation without corroborative evidence from other parts of the plant. However, since evidence from all organs and parts of the plant must be harmonized if a natural classification of plants is to be attained, evidence from wood anatomy should be given due consideration in taxonomy.

It should be emphasized, in conclusion, that the salient trends of evolutionary specialization in the cambium and xylem have been established by statistical analyses of the dicotyledons *as-a-whole*. In obtaining significant statistical averages from large volumes of randomly selected data, the effects of minor variations and localized divergent specializations are minimized. On the contrary, in dealing with the taxonomy of taxa of diminishing size, such variations and localized deviations become increasingly important. More attention should be devoted in the future to much neglected detailed investigations of the ranges of structural variability in individual plants and in individual species and genera. Furthermore, it is essential that anatomical data be obtained from plants of which herbarium vouchers are available.

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